THE AFFINITIES OF HOLCORPA MACULOSA SCUDDER AND OTHER TERTIARY MECOPTERA, WITH DESCRIPTIONS OF NEW GENERA

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In 1878, one year after the discovery of insects in the Florissant shales of Colorado, Scudder described from that formation a large and well preserved scorpion-fly, *Holcorpa maculosa*, belonging to the family Panorpidæ. He realized that the insect was a close relative of Panorpa, but believed that it differed from the members of that genus by the total absence of cross-veins in the wings. He also thought that the specimen was a male with a long, slender abdomen, although the genital bulb on the terminal segment was not preserved. In 1926 Professor T. D. A. Cockerell published a rough sketch of another specimen of this insect in his "Zoology of Colorado," showing the whole abdomen, head, and other parts which invited further study and which indicated that a detailed description of this new fossil was very desirable. Professor Junius Henderson, curator of the Natural History Museum at the University of Colorado, kindly forwarded the specimen to me for this purpose and I am indebted to him, as well as to Professor Cockerell, for the opportunity of investigating the affinities of this remarkable insect.

Scudder's type specimen of *Holcorpa maculosa,* which is now at the Museum of Comparative Zoology, shows clearly the color pattern of the wings and the details of the venation. Under proper illumination and magnification the cross-veins in the apical region of the wings can easily be seen, although Scudder was unable to discern them and designated their supposed absence as the distinctive characteristic of the genus Holcorpa. The type fossil is not a male, as Scudder thought; the abdomen is slender and tapering, as in all female Panorpidæ, and is utterly different from that of the male which Professor Cockerell secured. The new fossil is one of the most perfectly preserved Florissant insects which I have seen (Fig. 1). The two right wings are spread out, showing with surprising clearness the color

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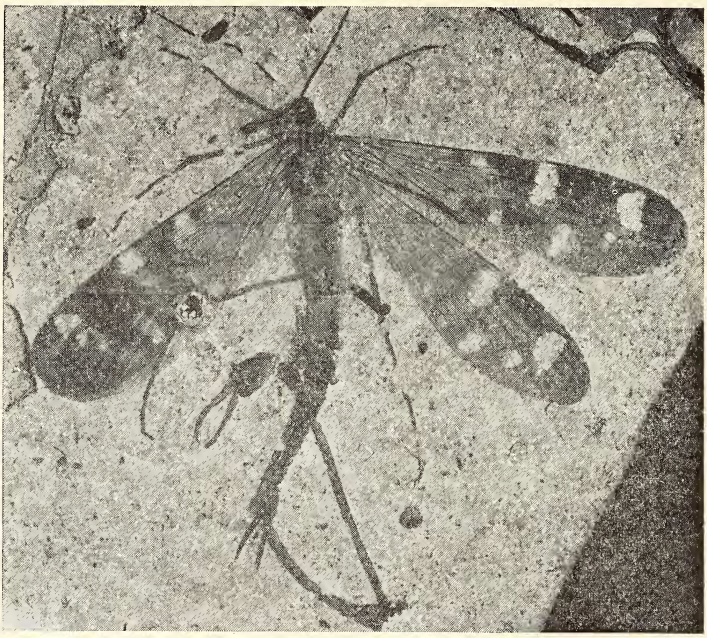


FIG. 1. Photograph of allotype of *Holcorpa maculosa* Scud. (×2).

markings, venation, and even the microtrichia on the wing membrane. The entire body, including antennæ, rostrum, legs, and many details of the genital bulb, is preserved. This complete preservation enables us to fix accurately the characteristics of Holcorpa and to form a more definite conception of the affinities of the genus with existing groups.

Genus *Holcorpa* Scudder

Holcorpa Scudder, 1878, Bull. U. S. Geol. Surv. Terr., 4: 542
1890, Tert. Ins. N. Amer., 174

Allied to Leptopanorpa and Neopanorpa. Rostrum long and slender; antennæ slender, with about forty segments; sixth, seventh, and eighth abdominal segments greatly modified and elongate; genital bulb large; Sc terminating on the costal margin; Rs with six branches in both pairs of wings; M with five branches in both wings; 1A long, extending beyond the origin of Rs.

Genotype: *Holcorpa maculosa* Scudder.

Holcorpa maculosa Scudder

(Plate XXXIII)

Holcorpa maculosa Scudder, 1878, Bull. U. S. Geol. Surv. Terr., 4: 542
Scudder, 1883, Ann. Rep. U. S. Geol. Surv. Terr., 12: 283
Scudder, 1885, In Zittel's Handb. Paleont., 1 (2): 778, fig. 984
Scudder, 1886, In Zittel-Barrois' Traité de Paleont., 2: 778, fig. 1001
Scudder, 1890, Tert. Ins. N. Amer.: 174–175; pl. 14, fig. 4, 5
Handlirsch, 1908, Foss. Ins.: 911

♂. Fore wing: length, 21 mm.; width, 6 mm. Hind wing: length, 18 mm.; width, 5 mm. Length of whole insect, 55 mm. Wing membrane dark brown or possibly black distally, hyaline basally; three large, irregular hyaline spots along the anterior margin, and three smaller ones near the posterior border, all in the distal half of the wings; sixth abdominal segment slender, about three times as long as the fifth and bearing posteriorly a pair of long horns, similar to those of *Neopanorpa cornuta* Esben-Petersen, but much larger; seventh segment about as long as the sixth and even more slender; eighth segment about one and one-half times as long as the seventh and a little more slender; posteriorly, at the junction with the genital bulb, the eighth segment is slightly swollen; genital bulb large, the basal part twice as long as wide; the forceps are longer than the rest of the bulb and are very slender and straight, without the basal tooth.

♀. Fore wing: length, 19 mm.; width, 5 mm. Hind wing: length, 17 mm.; width, 5 mm. Length of body, 30 mm. Wing markings similar to those of male; abdomen tapering, unusually long; the segmentation of the abdomen is not clear in the fossil.

Holotype (♀): No. 247, Museum of Comparative Zoology (collected by Mrs. Fisher).

Allotype, by present designation: No. 4494, University of Colorado, Natural History Museum (collected by Geo. N. Rohwer at Station 14).

There are several features of this insect which deserve comment. The general habitus of the male, which is by far the most important sex for taxonomic purposes, is shown in the photograph, figure 1. The terminal abdominal segments are directed anteriorly, and cross over the base of the preceding segment, indicating that at the time of its death the insect held the end of its abdomen in the usual panorpid position, curved upwards and over the rest of the abdomen. The head is turned sidewise to the left and is preserved in a lateral view. The tenuity of the sixth, seventh, and eighth abdominal segments of the insect is remarkable, for only one recent panorpid, *Leptopanorpa longicauda* Weele (Java) has a habitus at all comparable; but in this species the sixth segment is the longest and the eighth is the shortest of the three, the reverse of the condition in *Holcorpa maculosa.* The pair of horns on the posterior end of the sixth abdominal segment is another bizarre feature. As shown in the photograph, the seventh segment arises between these two horns. Only one existing panorpid, *Neopanorpa cornuta,* has similar structures and here the horns are very short and blunt; all other panorpids possess either a single median or none at all. The genital bulb is a well developed structure and the elongate forceps are unique among the Panorpidæ, but find their nearest approach among some of the Neopanorpas. The wing markings are more like those of certain Neopanorpas (*e.g., ocellaris* Navas) than those of Panorpa. It is certain that no Mecopteron related to Holcorpa exists in North America at the present time, and this statement also applies to South America, for the subfamily Panorpinæ has not been found there. In so far as the body structure is concerned it is nearest to Neopanorpa and perhaps Leptopanorpa, although both of these genera are restricted to the Old World, the former to Java, Borneo, and associated regions, and the latter to this same area and Japan. The presence of a member of the Panorpidæ in Colorado during the Miocene is not very surprising, even though the family extends in North America only a little west of the Mississippi River at the present time; but that this representative should show closest affinities with Old World genera, rather than our own, is most interesting. From a survey of the body structure of Holcorpa,—its

long rostrum, and extreme modification of the abdomen,—we are forced to the conclusion that this Miocene insect had already reached a position far from the primitive end of the panorpid line of descent. But when we examine the venation, we find a very different set of facts. In the subfamily Panorpinæ, which includes Panorpa, Neopanorpa, Leptopanorpa, and Panorpodes, the radial sector possesses five branches (R2a, R2b, R3, R4, R5), although a four-branched condition, in which R2 is simple, occurs irregularly and sporadically in some specimens. The media is always four-branched (M1, M2, M3, M4). Now in Holcorpa, as we have noted above, Rs possess six branches, R2a being deeply forked; and M has five branches, the extra branch being attached to M4. Nowhere among the recent Panorpidæ do we meet with an approach to this condition, except in the genus Chorista, where the media of the fore wing has five branches. In the hind wing of Chorista, however, the media has only four branches, as in other members of the family, and the radial sector of both wings consists of four branches. Since it has already been established by several investigators that the primitive and basic condition of the venation of the Mecoptera included a six-branched radial sector and at least a five-branched media, Holcorpa is placed by its venation near the very bottom of the panorpid series, although the body structure puts it close to the top.

The interesting affinities of Holcorpa, together with the condition of its venation, lead us to consider the other fossil Mecoptera belonging to recent families. Four species have been referred to the family Panorpidæ, and five to the Bittacidæ; these are included in the following synopsis:

Family Panorpidæ

ELECTROPANORPA, new genus.

Allied to Panorpodes. Beak short and stout; 6th, 7th and 8th abdominal segments not modified; wings with a six-branched Rs, and a five-branched M.

Genotype: *Panorpa brevicauda* Hagen.

Electropanorpa brevicauda (Hagen)

Panorpa brevicauda Hagen, 1856, in Berendt's Berst. befindl. organ. reste. vorw., 2(1): 91; pl. 8, fig. 21.

Panorpa brevicauda Handlirsch, 1908, Foss. Ins.: 911.

This species was based upon a male specimen from the Baltic amber (Oligocene). Hagen states that the head has the ordinary configuration of a Panorpa, although the beak is stout and shorter. His figure of the abdomen shows that the 6th, 7th, and 8th segments are unmodified, like those of Panorpodes. This feature alone eliminates the species from Panorpa. The wing venation is especially interesting, because we again find the condition which was present in Holcorpa,—a six-branched Rs, and a five-branched M. Consequently although its shortened beak and abdominal structure place *brevicauda* close to Panorpodes, the wing venation requires that it be assigned to a separate genus, and for this reason Electropanorpa is established.

Family Bittacidæ.

ELECTROBITTACUS, new genus.

Allied to Bittacus. Rostrum greatly reduced; venation identical with that of Bittacus.

Genotype: *Bittacus antiquus* Pictet.

Electrobittacus antiquus Pictet

Bittacus antiquus Pictet, 1854, Traité de paleont., 2nd ed., 2: 379; pl. 40, fig. 26.
Hagen, 1856, in Berendt's befindl. organ. reste. vorw., 2(1): 92; pl. 7, fig. 23; pl. 8, fig. 22.
Handlirsch, 1908, Foss, Ins.: 911.

This remarkable insect was originally described from two Baltic amber specimens, and Hagen subsequently obtained two additional specimens, both of which were splendidly preserved. The wing venation is the same as that of Bittacus, but the rostrum is exceedingly short, fully as small as that of Panorpodes. This characteristic at once eliminates *antiquus* from Bittacus and from all the other genera of the Bittacidæ. Only in certain species of Panorpodes (Panorpidæ) is the rostrum similarly abbreviated; and I believe that *antiquus* occupies a position in the family Bittacidæ analogous to that held by Panorpodes in the Panorpidæ.

Palæobittacus Carp.

Allied to Bittacus. Differs from Bittacus in the possession of a five-branched media, and a cross-vein between Rs and M at the base.

Genotype: *Palæobittacus eocenicus* Carp.

Palæobittacus eocenicus Carp.

Palæobittacus eocenicus Carp., 1928, Ann. Carnegie Mus., 18: 240–249; fig. 1; pl. 12.

This species was based upon a splendidly preserved specimen from the Green River Shales of Colorado (Eocene). The body structure is similar to that of Bittacus, but the media has the extra branch on M4 that we have seen in Holcorpa and Electropanorpa.

Probittacus Martynov.

Allied to Bittacus. M with five branches.

Genotype: *Probittacus avitus* Mart.

Probittacus avitus Mart.

Probittacus avitus Mart., 1927, Bull. Acad. Sci., U.S.S.R., 21: 661–665; fig. 11.

This important insect is known to us only by a well preserved fore wing from the Jurassic beds of Galkino, Turkestan, and is the only Mesozoic Mecopteron which can be referred to a recent family. Martynov originally placed it within the extinct family Neorthophlebiidæ, but the wing is identical with that of Bittacus, except for the extra branch on M4. The discovery of such an insect in the Jurassic, so close to an existing type, is very unexpected.

All the other fossil Mecoptera which have been referred to recent families must be eliminated entirely from the order or be temporarily placed in an uncertain position, until additional material has been secured. *Panorpa rigida* Scudder, from the Florissant shales, is too incompletely preserved to permit even family classification. *Panorpa arctiiformis* Ckll., also from the Florissant shales, is undoubtedly a member of the family Panorpidæ, but I have not seen the type specimen and there is nothing in the description to indicate its affinities. *Dinopanorpa*

megarche Ckll., from the Miocene of Siberia, is certainly not a member of the Panorpidæ, and may not even be a scorpion-fly. *Bittacus reticulatus* Heer, from the Miocene of Radoboj, was based upon a minute fragment of a wing which exhibits no mecopterous features whatever; and *Bittacus validus* Hagen, while possibly a Mecopteron, cannot belong to the Bittacidæ, for the venation is utterly different from that characteristic of the family.

From this survey of the fossil Mecoptera which belong to recent families, it is clear that only five species are completely enough known for us to determine their affinities: Probittacus, Electrobittacus, Palæobittacus, Electropanorpa and Holcorpa. But small as this list is, I believe that we can derive sufficient data from these fossils to throw some light on the evolution of the rostrum and the venation in the Bittacidæ and the Panorpidæ. For in both of the above representatives of the Panorpidæ (Holcorpa and Electropanorpa) the radial sector is six-branched and the media is five-branched, although the body structure is fully as highly specialized as that of the recent Panorpas. So

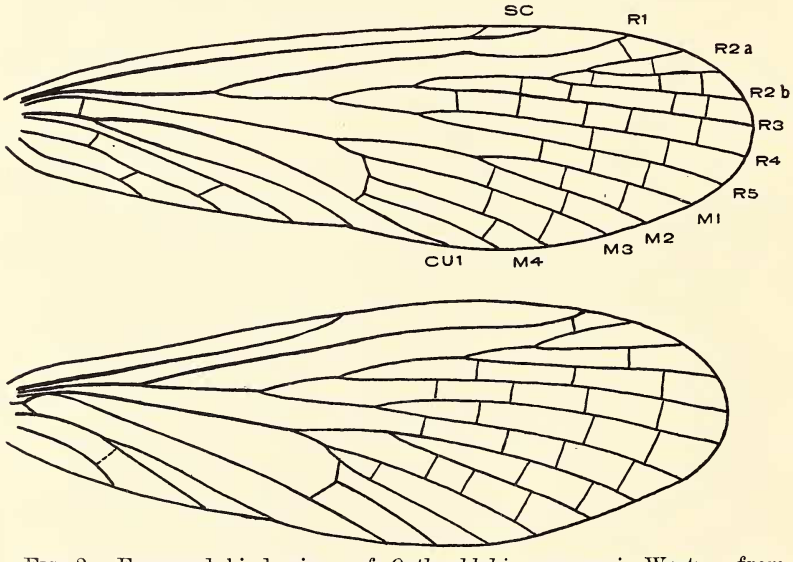


FIG. 2. Fore and hind wings of *Orthophlebia communis* Westw., from the Lower Lias of England; drawn from specimens in the Museum of Comparative Zoology.

far as the venation is concerned these two genera are practically identical with the Mesozoic Orthophlebias (Fig. 2) and are intermediate between them and the true Panorpidæ. This idea of the descent of the panorpids from the Orthophlebiidæ has long been established, but the point which I wish to emphasize here is that these Mesozoic Orthophlebiids *possessed a long beak similar to that of Panorpa.*[1] This is strong evidence that the short rostrum of Panorpodes is not a primitive trait, as usually supposed, but a specialized one, formed by the secondary reduction of the parts concerned. Enderlein came to this same conclusion many years ago from a brief survey of the phylogeny of the Mecoptera.[2] In the fossil Bittacidæ which we have just considered the radial sector has already been reduced to the four-branched condition, as in all living genera, but the media is still five-branched (except in Electrobittacus) the extra branch of M4 being best developed in the Jurassic Probittacus. The wings of these fossil genera are therefore intermediate between those of the true Bittacidæ and some of the Orthophlebiid types, which possessed a perfect rostrum. The condition of the rostrum in Electrobittacus is apparently another result of reduction and specialization, analogous to the situation in Panorpodes. All the fossil evidence available at the present time agrees in showing that the Panorpidæ were derived directly from the Orthophlebiids, gradually losing a branch of the radial sector and of the media, and also attaining in Panorpodes a complete reduction of the rostrum. The Bittacidæ seem to be a side-branch of the Orthophlebiids, having already acquired by the Jurassic a four-branched radial sector, but retaining the five-branched media until recent times, when the four-branched media has also become the normal.

This combination of specialized body structure and relative primitive venation in the fossil Panorpidæ and Bittacidæ points definitely to the conclusion, which has not previously been considered, that the evolution of the venation has lagged behind that of the body structure; and that the present body structure of the two families was already established by the middle Meso-

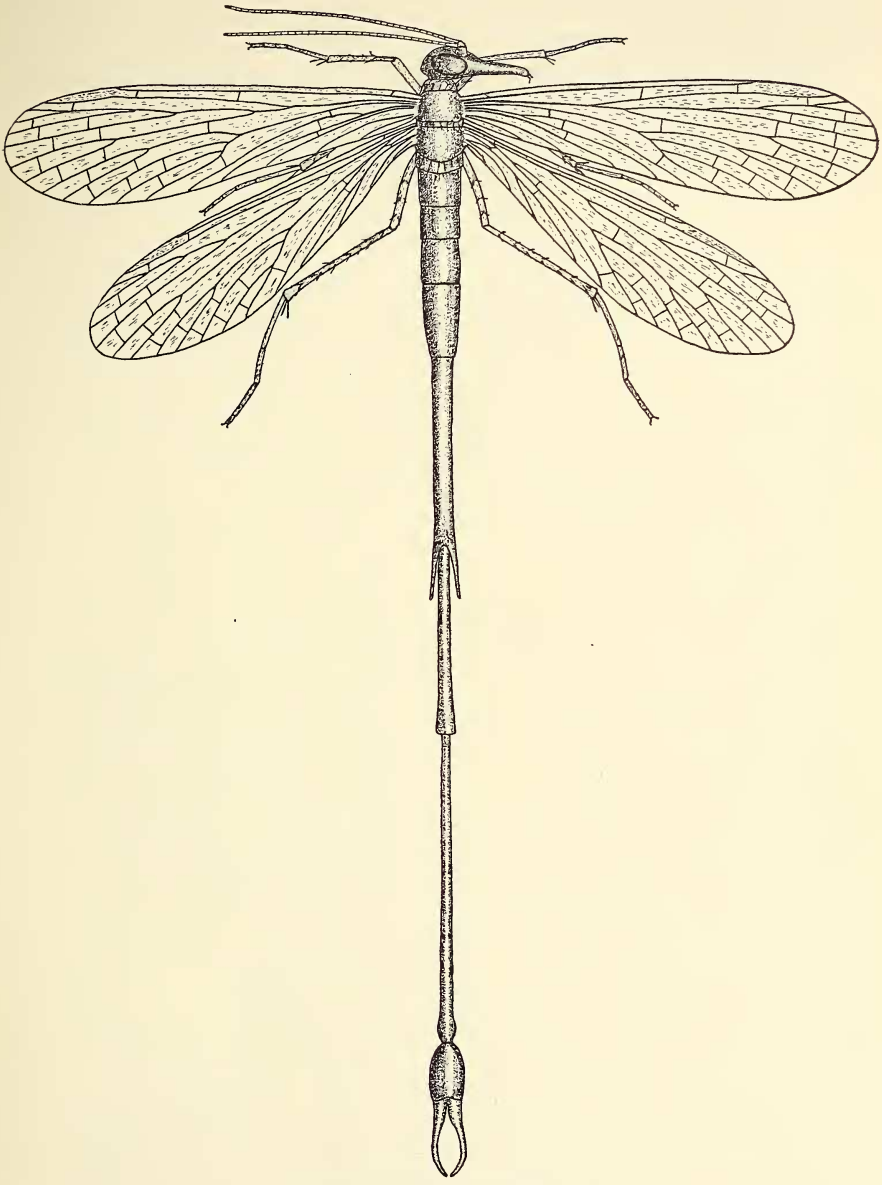
[1] See Martynov's figures, Bull. Acad. Sci. U. S. S. R., 21; 657.

[2] Zool. Anz.; 35 (12/13): 385–399, 1910.

zoic, although the venation was still in the process of modification. The body structure of *Holcorpa maculosa* is essentially so modern, even to the genitalia, that on this basis alone we might be tempted to determine the insect as a living species; but the venation is the same as that possessed by the Mesozoic Orthophlebias. This retarded modification of the venation in the Mecoptera enables us to trace the phylogeny of these insects more accurately by the wing venation than by the body structure.

PLATE XXXIII

Holcorpa maculosa Scudder, allotype. The abdomen has been straightened in order to show its extreme length. All structures figured here are preserved in the fossil.



HOLCORPA MACULOSA